DUSK CHORUSING BEHAVIOUR IN CICADAS (HOMOPTERA: CICADIDAE) AND A MOLE CRICKET, BRISBANE, QUEENSLAND

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Diurnal singing behaviour is documented for 9 SE Queensland cicadas from *Arunta*, *Psaltoda* and *Pauropsalta*, with particular reference to the presence/absence of dawn/dusk chorusing. This occurs more within relatively sedentary and also aggregating species. Detailed documentation of dusk chorusing during November 1996 -April 1997 in inner city St Lucia, Brisbane, is presented for 5 cicadas *Cystosoma saundersii* Westwood, *Glaucopsaltria viridis* Goding & Froggatt, *Tamasa tristigma* (Germar), *Abricta curvicosta* (Germar), and *Psaltoda claripennis* Ashton, and the mole cricket (*Gryllotalpa pluvialis* Mjöberg). The choruses closely follow, seasonally, the sunset and civil twilight curves, except for *T. tristigma* which systematically changes its pattern during the season. Extensive interspecific synchrony of chorusing occurs at the same location, although chorus start/finish times vary between species. Factors controlling chorusing behaviour, especially light intensity and ambient temperature, and the importance of the distinctive interspecific song characteristics, are discussed. ☐ *Cicadas, mole cricket, chorusing behaviour, Brisbane.*

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Many southeastern Queensland (SEQ) cicadas exhibit both extended daytime singing plus short and intense bursts of dawn and/or dusk chorusing. Certain species are crepuscular, with singing restricted to dusk, the best known local example being the Bladder Cicada, *Cystosoma saundersii* Westwood. Not all cicadas, however, exhibit dawn/dusk chorusing and observations over 30 years suggest that the behaviour is best developed in: 1) relatively localised and sedentary cicada species, and 2) aggregating species, many of which are also localised.

Comparable dawn/dusk chorusing behaviour is documented worldwide, including Malaysia (Gogola & Riede, 1995); New Mexico (Crawford & Dadone, 1979); Tennessee (Sanborn, 2000); Mexico (Moore, 1962); Borneo (Riede, 1996, 1997; Reide & Kroker, 1995); Costa Rica (Young 1976; 1982:102); Thailand (Gogola, 1995); Fiji (Duffels, 1988); Southern Africa (pers. obs.). Myers (1929: 206-7, 221) quoted further examples from South America, New Zealand, the Philippines and the Himalaya.

The main feature of these choruses are their short, but predictable (day to day) timing and duration, and their intensity. Only severe late afternoon storms seem to modify their timing. In SEQ, strongly mobile cicada species rarely produce defined dawn/dusk choruses, but instead sing more or less continuously throughout the day from early morning to near dusk.

This report outlines observed cicada singing behaviour in a variety of species in SEQ and, in particular, more detailed documentation, over 6 months, of dusk chorusing of 5 cicada and 1 Orthopteran species from suburban St Lucia, central Brisbane (27°29.63'S, 153°00.04'E). All 6 species could be heard singing synchronously within the same localised area. This account starts by reporting more general observations of diurnal singing patterns in SEQ.

DIURNAL CICADA SONG PATTERNS

Two widespread but relatively sedentary mangrove-inhabiting cicadas, *Arunta interclusa* (Walker) and *Psaltoda plaga* (Walker), provide examples of both strong day and dawn/dusk chorusing (Fig. 1). Both species are medium to larger sized cicadas (♂ body lengths [MBL] 27-33 and 27-39mm, respectively) with relatively sedentary behaviour patterns. Both exhibit strong diurnal singing, starting between 0600-0700 hours (Eastern Standard Time), with progressive reduction in intensity during mid to late afternoon until cessation at approximately 1700 hours. Dusk chorusing occurs immediately following sunset, being less intense for *P. plaga*. Dawn chorusing commences immediately prior to sunrise. Although dawn chorusing is more poorly developed in *P. plaga*, it commences its

Eastern Standard Time - Based on observations over 12 days
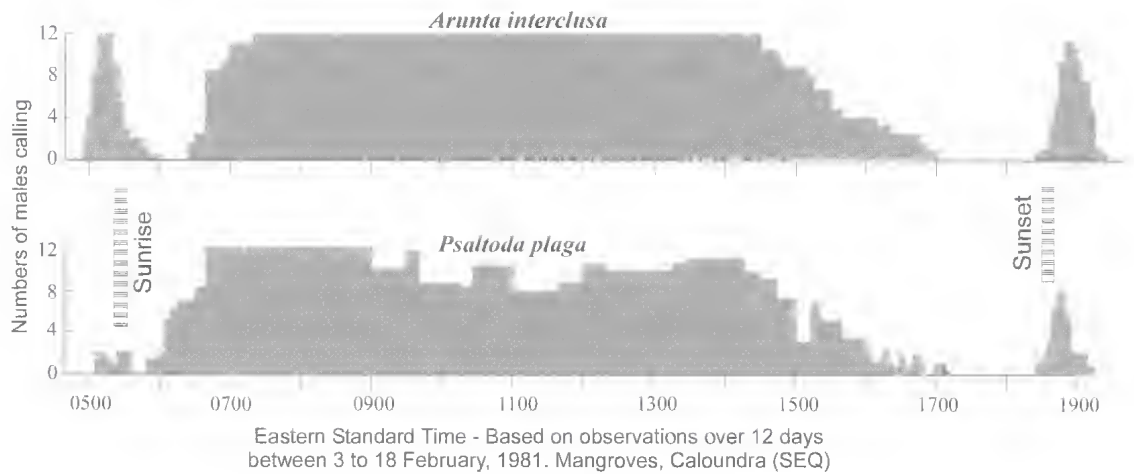between 3 to 18 February, 1981. Mangroves, Caloundra (SEQ)

FIG. 1. Daytime singing patterns of two mangrove dwelling cicadas. The graphs are compiled from regular daily observations, at intervals of 15-20 minutes, of times at which songs of each species are heard within a given habitat. The sunrise/sunset times are shown for the period of observation.

diurnal singing slightly earlier than *A. interclusa*. *P. plaga* normally forms relatively dense singing aggregations with short but frequent flights, this behaviour being less pronounced in *A. interclusa*. Both species sing from inner and outer mangrove branches which allows micro-habitat selection for variable shade conditions. Mangroves, in fact, are subjected to direct and also indirect solar radiation from reflection off surrounding water and wet mud surfaces. The afternoon decrease in song activity is presumably a behavioural response by the insects to avoid superheating (i.e. exceeding thermal tolerances; Sanborn, 1997).

Psaltoda claripennis Ashton, *Psaltoda harrisii* (Leach) and *Tamasa tristigma* (Germar) (Fig. 2) illustrate further examples of song patterns. Both *Psaltoda* species are medium to larger sized cicadas (MBL 24-34 and 22-29mm, respectively) and widespread throughout SEQ. *P. claripennis* forms localised singing aggregations in suburban and open forest habitats while *P. harrisii* is restricted to open forest and wallum communities, again normally in localised aggregations. *P. claripennis* produces a strong dusk chorus, but no dawn chorus, whereas *P. harrisii* surprisingly exhibited neither during the observation period. Both are strong diurnal singers, with *P. claripennis* showing a marked reduction of song intensity during the midday period. As both species sing from exposed tree branches, reduction and later afternoon cessation of song seems to represent behavioural thermoregulation and allow feeding (Sanborn, 1997). *T. tristigma* is a very

Eastern Standard Time - Based on observations over 19 days between
25 January to 20 February, 1983. Open forest, S.W. Brisbane (SEQ)
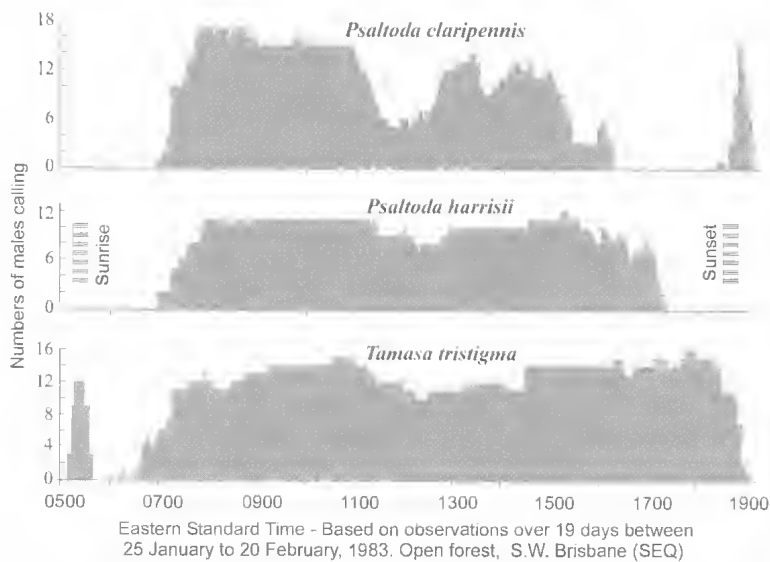
FIG. 2. Daytime singing patterns of three open woodland/suburban cicadas. Data compiled as in Fig. 1.
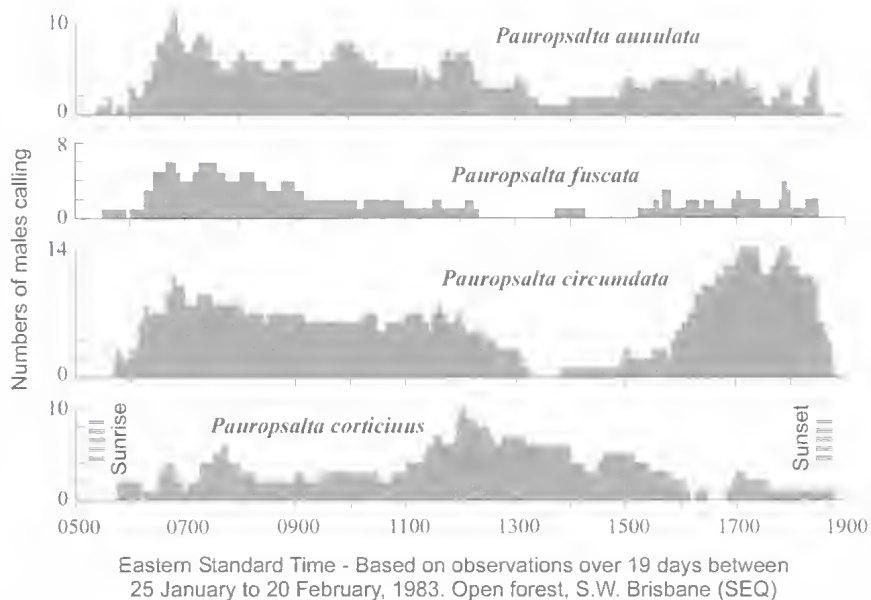
FIG. 3. Daytime singing patterns of four open woodland *Pauropsalta* cicadas. Data compiled as in Fig. 1.

common, medium sized (MBL 16-23mm), rather sedentary species of open forest and suburban areas. Singing occurs from exposed tree trunks. It exhibits a strong dawn chorus (coinciding with sunrise), followed at about 0700 by the beginning of the extended diurnal song period. This cicada is also notable for the fact that it regularly sings strongly during rain. As shown below, the late afternoon to dusk singing behaviour changes from early summer through to autumn, with discrete dusk chorusing only occurring early and late in a given summer season.

Singing patterns of 4 *Pauropsalta* species (Fig. 3) show further variations. *P. fuscata* Ewart, *P. corticinus* Ewart and *P. annulata* Goding and Froggatt (MBL 12-17, 14-18 and 11-15mm, respectively) are small, cryptic and highly mobile species, common in open forests and wallum habitats (Ewart, 1989). *P. annulata* is a foliage dweller, while *P. fuscata* and *P. corticinus* provide good examples of 'sing and fly' behaviour (e.g. Sanborn, 1997; Duffels, 1988: 74). Singing occurs from open tree trunks and branches, posts, etc., where their dominantly black coloration facilitates thermoregulation from solar radiation, with additional endogenous heat provided from frequent flight activity (e.g. Sanborn, 1997, 2000). Singing occurs throughout the day, extending to late afternoon, but they do not exhibit discrete dawn/dusk chorusing. This is believed to result from their smaller body size which precludes significant heat retention once

solar radiation ceases to be effective (M. Coombs, pers. comm.).

Pauropsalta circumdata (Walker) is a slightly larger (MBL 18-21mm) member of the genus, relatively sedentary, singing from open branches of medium to tall eucalypts, usually well exposed to solar radiation. No discrete dawn/dusk chorus is emitted. Diurnal song production extends through the morning, with a clear period of suspended activity during early-mid afternoon, followed by intense singing from late afternoon extending to dusk. This final phase incorporates the 'dusk chorus' time interval. During this late afternoon/dusk phase, the insects remain exposed to the sun allowing them to sing until solar radiation effectively ceases.

EVENING CHORUS SYNCHRONY IN FIVE CICADA AND ONE MOLE CRICKET SPECIES

Start and finish times for the dusk choruses of *Glaucopsaltria viridis* Goding & Froggatt (Bottle Cicada), *C. saundersii* (Bladder Cicada), *Abricta curvicosta* (Germar) (plus *P. claripennis*), *T. tristigma*, and the mole cricket *Gryllotalpa pluvialis* Mjöberg, are illustrated for a 6 month period (Figs 4-6). Each species sang within a localised suburban habitat, the songs each being easily heard from the single observation location. The choruses are compared with sunset and civil twilight times (data from Astronomical Applications Dept., U.S. Naval
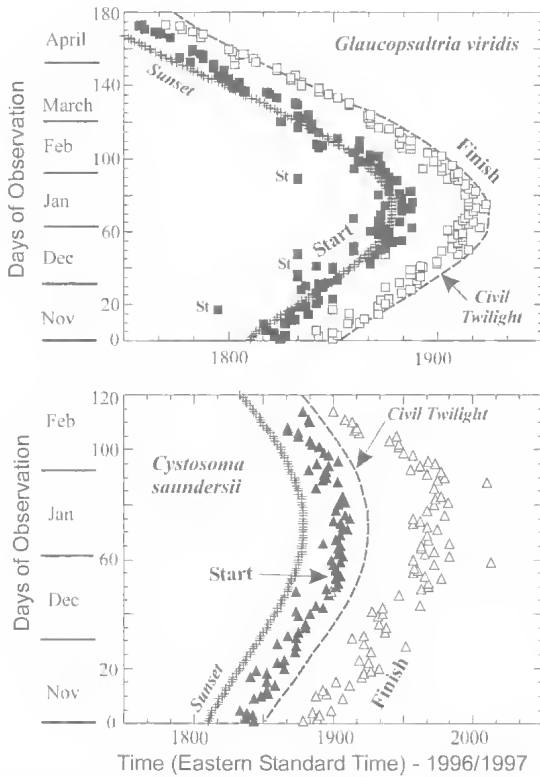
FIG. 4. Dusk singing patterns, over 4-6 month intervals, of *G. viridis* and *C. saundersii*, from St Lucia, Brisbane City. The solid symbols indicate start, and hollow symbols finish, of dusk choruses. 'St' against a symbol indicates storm. Sunset and civil twilight curves are plotted for comparison.
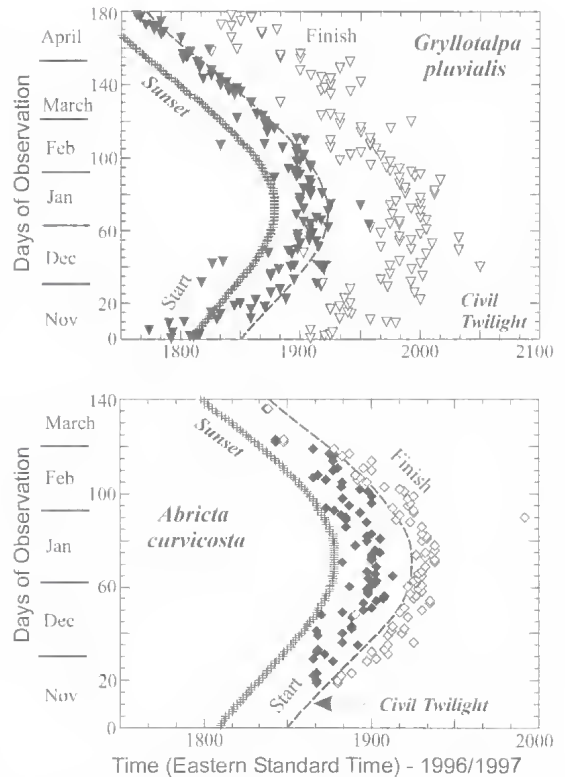
FIG. 5. Dusk singing patterns, over 5-6 month intervals, of *A. curvicosta* and the Common Mole Cricket, *G. pluvialis*. Filled and hollow symbols indicate start/finish of dusk chorusing. Sunset/civil twilight curves are shown for comparison.

Observatory, Washington). The plots highlight the close correspondence between the seasonally changing dusk chorus timing and light intensity. Sunset is formally defined as the moment the uppermost point of the sun appears to vanish below the horizon and civil twilight as the time between sunset and the moment the sun reaches a point lying 6° below the horizon (Beck, 1980; Nielsen, 1963).

Although a similar result could no doubt be obtained with sky light intensity measurements (e.g. Crawford & Dadone, 1979), such measurements do not allow for the differing micro-habitat niches of the cicadas. *C. saundersii* and *G. viridis* are both cryptic, green, crepuscular species which inhabit dense foliage, whose main song periods are at dusk (see also Doolan & MacNally, 1981; *G. viridis* does produce brief singing and clicking during the day, especially when overcast). *C. saundersii* and *G. viridis* are large to medium sized cicadas (MBL 39-53 and

26-35mm, respectively) with abnormally enlarged abdomens, and consequently relatively poor flight. *A. curvicosta* (MBL 25-31mm) occurs on tree trunks, normally partly hidden by foliage, while *P. claripennis* and *T. tristigma* sing from more open tree trunks and branches. The mole cricket occurs in shallow soil burrows. Absolute light intensities will vary within these different microhabitats at any given time. Nevertheless, the mole cricket data are less regular than the corresponding cicada data, possibly due to variable diurnal and seasonal shadow effects over their fixed burrow positions. Rain flooding of their burrows presumably explains 'non-singing' during and following afternoon storms. The dusk chorusing of *P. claripennis* overlapped extensively with, and was largely masked by the singing of *A. curvicosta*. Although the 2 species commenced dusk chorusing nearly simultaneously, *P. claripennis* stopped earlier.
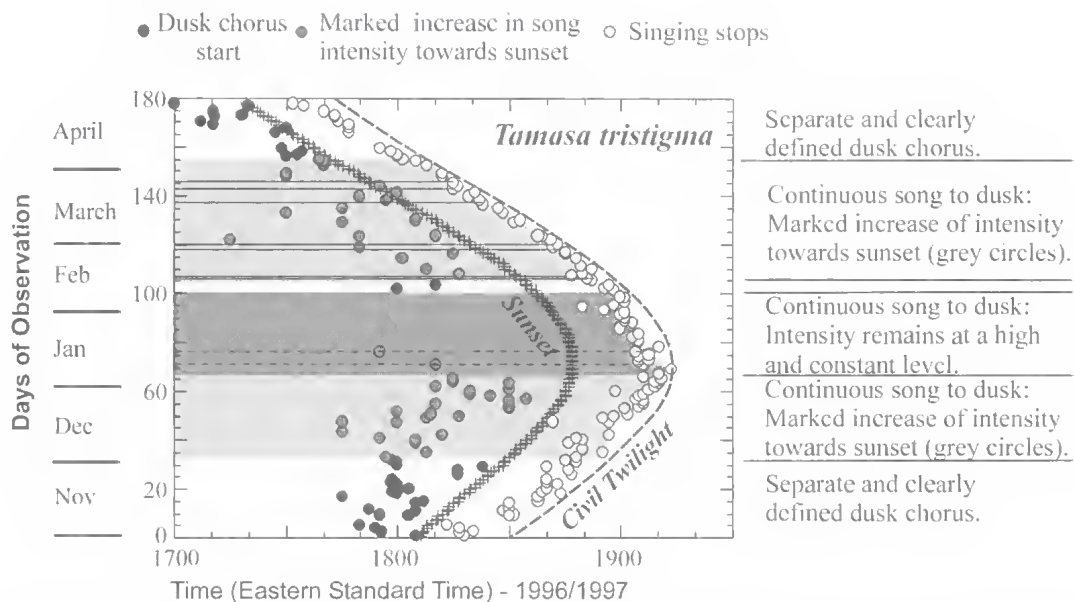
FIG. 6. Dusk singing patterns, over 6 month interval, of *T. tristigma* showing the seasonal changes of afternoon/dusk singing behaviour, noting that singing cessation is consistent throughout. The solid and dotted lines represent isolated days of anomalous singing behaviour relative to each behavioural segment. True dusk chorusing is restricted to early and late in season. Sunset/civil twilight curves are shown for comparison. See also Fig. 8D.

T. tristigma shows a systematic change of singing patterns from early summer through to autumn (Fig. 6). Discrete dusk chorusing occurs in early and late summer season (November and April), with a very brief additional occurrence in early February. In mid-summer (mostly January), singing is continuous at relatively high intensities through until near civil twilight. The periods either side of mid-summer (December and February/March) have continuous singing through to civil twilight, but with marked increases in intensity in late afternoon/dusk (i.e. intermediate behaviour to discrete dusk chorusing). At all times during summer, however, singing consistently ends close to the civil twilight curve, irrespective of whether a discrete dusk chorus, or continuous late afternoon to dusk singing occur.

Although clearly correlated with fading light, triggering mechanisms of dusk chorusing may be more complex. These include (Crawford & Dadone, 1979; Riede & Kroker, 1995): i) total light intensity; ii) rate of change of light intensity: iii) changing spectral composition of evening light, such as the suppression of middle wavelengths of visible light (Endler, 1992); and iv) barometric pressure changes prior to dusk.

Some support for a more complex triggering mechanism, for start of dusk chorus, is provided by the lack of statistically significant differences between fine to cloudy/overcast days (Table 1), although the means do show systematic shifts. Only severe late afternoon storms caused the early onset of dusk chorusing (points labeled 'st' in Fig. 4). Another relevant aspect is the small seasonal variation of twilight period (i.e. between sunset and civil twilight), 0.40-0.47 hour for the total observation period.

The close correlations between start and finish of dusk choruses and sunset/civil twilight curves, for each species, are illustrated further by Pearson correlation coefficients (r) derived from the linear plots between these variables (e.g. Fig. 7D). The coefficients between sunset and chorus start (finish) times or *G .viridis, C. saundersii, T. tristigma, A. curvicosta* and *G. pluvialis* are, respectively, 0.96 (0.99, n=121); 0.95 (0.88, n=84); (0.99, finish only, n=121); 0.85 (0.88, n=76); and 0.89 (0.86, n=117). Identical values are calculated using civil twilight instead of sunset times. The correlation coefficients are high, especially those for *T. tristigma* (chorus finish), *G. viridis*, and chorus onset of *C. saundersii*, pointing to absolute light intensity as

TABLE 1. Dusk chorus starting times, relative to sunset, under clear and cloudy conditions, chorus duration's, reference CREP data, ambient temperatures (T_a) and temperature gradients during dusk chorusing. Data presented as means and standard deviations (in parentheses). * Chorus finish only.

	T. tristigma	G. viridis	C. saundersii	A. curvicosta	G. pluvialis
(Chorus start – sunset) (hrs). All data	0.32 (0.07)*	0.030 (0.11)	0.26 (0.06)	0.24 (0.09)	0.29 (0.21)
(Chorus start – sunset) (hrs). Clear to <50% cloud cover	-	0.075 (0.071) (n = 77)	0.28 (0.052) (n = 46)	0.26 (0.086) (n = 39)	0.33 (0.16) (n = 74)
(Chorus start – sunset) (hrs). Overcast to >50% cloud cover	-	-0.031 (0.12) (n = 44)	0.23 (0.068) (n = 38)	0.22 (0.086) (n = 37)	0.23 (0.26) (n = 43)
Chorus duration (hrs). All data	-	0.33 (0.09)	0.61 (0.16)	0.29 (0.14)	0.87 (0.34)
CREP; chorus start. All data	-	0.087 (0.25)	0.59 (0.15)	0.54 (0.20)	0.68 (0.49)
CREP: chorus finish. All data	0.74 (0.16)	0.86 (0.13)	1.97 (0.35)	1.19 (0.27)	2.69 (0.56)
T_a at chorus start (°C). All data	24.2 (1.9)	23.8 (1.7)	23.6 (1.8)	24.0 (1.5)	23.5 (1.7)
T_a at chorus finish. (°C). All data	23.5 (1.7)	23.5 (1.7)	23.3 (1.8)	23.8 (1.5)	23.0 (1.8)
Temperature gradient during dusk chorus (°C). All data	0.8 (0.8)	0.3 (0.4)	0.3 (0.6)	0.2 (0.3)	0.9 (0.8)
Total T_a range during dusk chorus (°C)	18-30	19-29	18-29	21-27	18-29
n (number of data)	121	121	84	76	117

the dominant control on the timing of dusk chorusing. The coefficients for *C. saundersii* (finish), *G. pluvialis* and to a less extent *A. curvicosta,* are numerically lower, reflecting the fact that chorusing ceases well after twilight, indicating additional controlling factor(s). Even for *G. viridis,* there is a discernible deviation of the chorus starting time, relative to sunset, early and late during the summer season (Fig. 7D). This also suggests secondary controlling factors, possibly seasonally changing spectral properties of the evening light. An alternative time parameter that has been advocated for such studies is the crepuscular time unit (CREP; Nielsen, 1963; Beck, 1980). Although noted in Table 1, this parameter was not found to be as useful in this study as simpler comparative plots using standard sunset and twilight data.

The possible influence of ambient temperature (T_a) and temperature gradients on chorusing patterns are evaluated from temperature data, taken every 30 minutes during the whole period of observation, from records for Brisbane from the Australian Bureau of Meteorology. These data were linearly extrapolated to the seasonal starting and finishing times of chorusing for each species. T_a ranged between 18-30° during chorusing, averaging between 23-24° (Tables 1 and 2) during the 6 month observation period. These temperature ranges suggest that T_a is not a controlling factor in triggering or controlling the duration of dusk (or dawn) chorusing. This is confirmed, for all 5 species, by the lack of

significant correlation's between the start and finish of dusk choruses and T_a (r values range between –0.22 and 0.42) or between temperature gradients during chorusing and the start/finish timing of the choruses (r values –0.24 to 0.35). It is recognised, however, that for singing to occur, body temperature needs to exceed some critical minimum value for each species (Sanborn, 1997, 2000), although this is in part controlled by T_a. Josephson & Young (1979) indicated that *C. saundersii* ♂ ♂ are ectothermic. It is unknown whether this also applies to the other cicadas considered here. Nevertheless, the patterns of singing behaviour and habitats of *G. viridis* and *T. tristigma* males suggest possible ectothermy.

Chorus duration (Fig. 7A; Table 2) for *C. saundersii* increases during the summer season, but sharply decreases at the end of its season, believed to reflect a combination of slightly shorter twilight period and especially the diminishing and aging population. *G. viridis,* and *A. curvicosta* exhibit shorter chorus lengths both early and late in the season (Fig. 7B,C; Table 2), thought to also reflect smaller population and twilight length effects. *G. pluvialis* shows no systematic seasonal change of chorus length. Reference to the seasonal variation of T_a's for dusk chorus finish (≈start) times for *G. viridis* (Fig. 8A) suggest that seasonal T_a variations could have a significant effect in determining seasonal changes in chorus duration. This is negated, however, by: i) the lack of significant correlation's, for all five species, between chorus
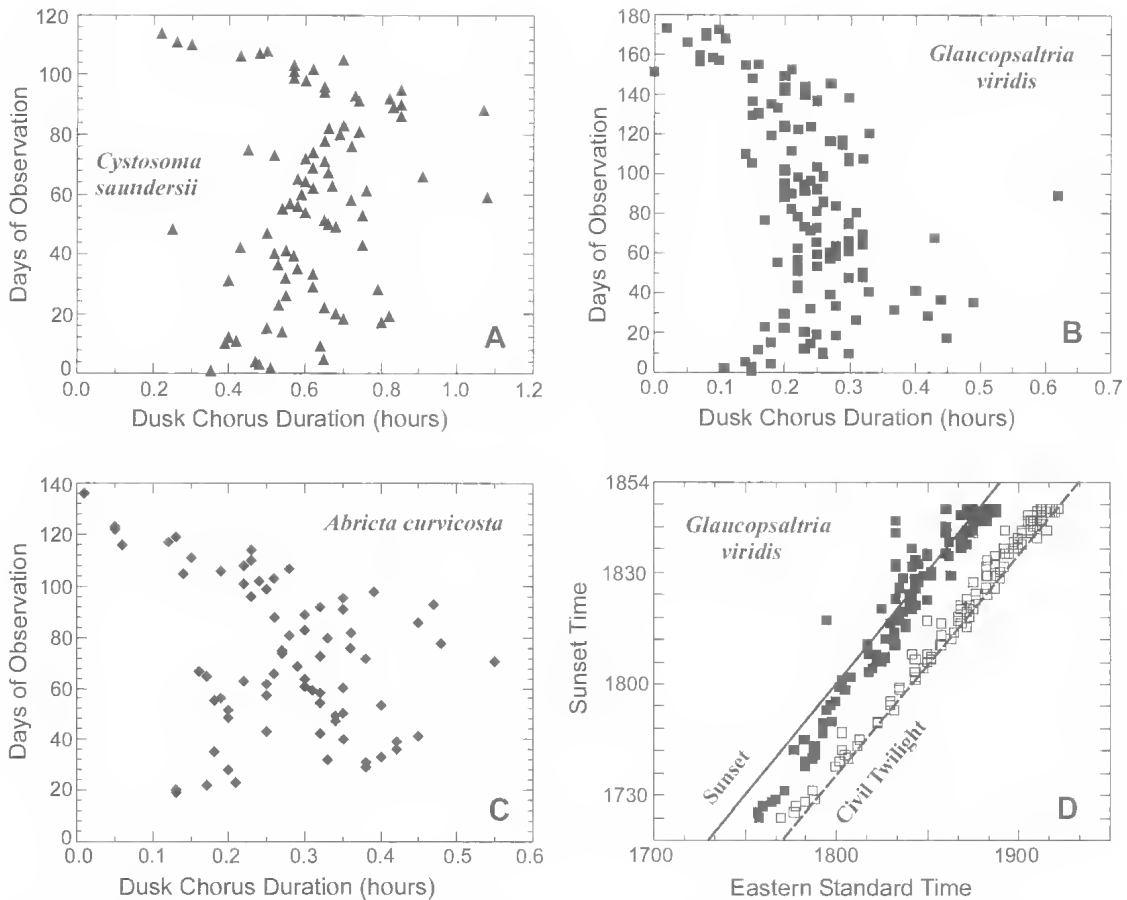
FIG. 7. A-C, dusk chorus duration in relation to progress of season (days of observation starting on 1 Nov, 1996, as in Figs 4 to 6). D, linear plot of sunset and twilight times in relation to the start/finish (filled/hollow symbols) of the dusk chorus of *G. viridis* over 6 month interval (as in Fig. 4).

duration and either start/finish T_a's (r values of –0.20 to 0.28), or temperature gradients during choruses (r values 0.06 to 0.43); ii) although *A. curvicosta* and *C. saundersii* populations collapsed before those of the other 3 species, plots of days of observation (= season) versus T_a's of chorus finish (≈start) for both of these species show no corresponding late season decrease in T_a (e.g. Fig. 8B, illustrating the data for *C. saundersii*); iii) T_a data for *G. pluvialis* show late season decreases (Fig. 8C), yet no corresponding decrease in dusk chorus duration is found (although in this case, the subsurface micro-habitat is a complicating factor).

Synchrony: A high degree of synchrony occurs between the 6 insect species during dusk chorusing (Figs 3-6). A general time progression occurs from *T. tristigma* to *G. viridis, A.*

curvicosta (+ *P. claripennis*) to *G. pluvialis,* (Fig. 9). Mean chorus duration (Table 1) ranges from 0.29 (*A. curvicosta*) to 0.87 hour (*G. pluvialis*), whjch are consistent with dusk chorusing observations in Malayasian and Bornean rainforests (Gogola & Riede, 1995). Only the pre-sunset part of thc *T. tristigma* song and the later part of the *G. pluvialis* chorus do not overlap with competing insect songs. The late afternoon to early evening period is an acoustically 'busy' period of the day, from spring through to autumn, particularly as birds are also acoustically active during the same time period. This implies that the temporal structures and frequencies of the songs of the respective insects are sufficiently species specific to enable mate recognition to occur, as further outlined below.
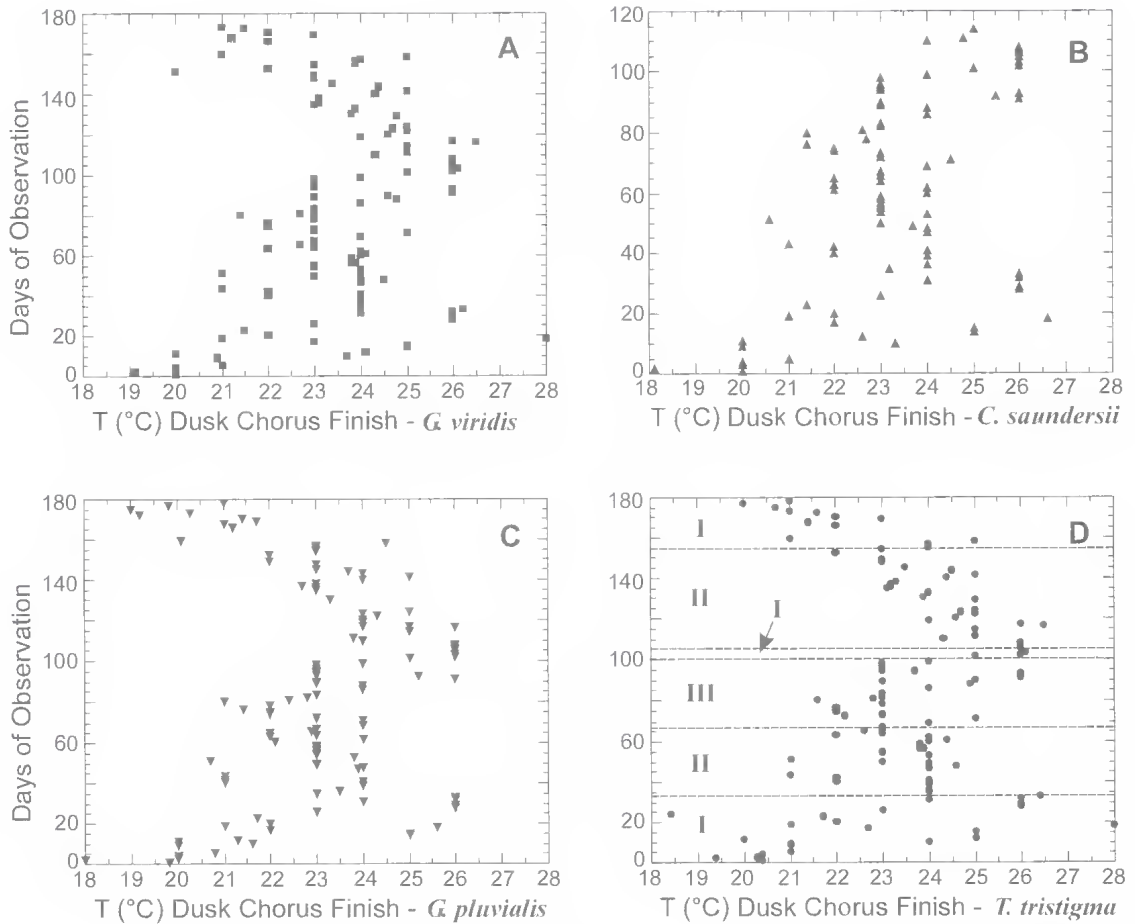
FIG. 8. Seasonal (days of observation) variation of ambient temperatures (T_a) at the cessation of dusk chorusing for : A, *G. viridis* (Fig. 4); B, *C. saundersii* (Fig. 4); C, *G. pluvialis* (Fig. 5); and D, *T. tristigma*. In (D) the phases of changing singing behaviour are shown, based on Fig. 6, as follows: I, discrete dusk chorusing; II, continuous afternoon singing through to dusk, with marked intensity increase near sunset; III, continuous song through to dusk, with no change in song intensity.

DISCUSSION

Henwood & Fabrick (1979) highlighted, with particular reference to vertebrates, the optimal acoustic environment provided within the dawn chorus window, e.g. reduced temperature gradients, low wind and wind gradients, and low abiotic noise. This is expected to lead to more efficient broadcast coverage and therefore significant advantages to individuals selecting the early morning calling environment. Young (1981) pointed out that the same data indicate that dusk is also a time of low background noise and relatively stable wind and temperature gradients

and again may lead to an adaptive advantage towards dusk chorusing.

The underlying reasons for dusk/dawn chorusing in many cicadas are still unknown, but the following points are relevant to the phenomenon: i) Not all cicadas exhibit such behaviour, which seems to be most prevalent in more localised (static) species with continuous/monotonous calls. Dusk/dawn chorusing may not occur in smaller species (e.g. some *Pauropsalta*) due to more rapid heat loss once solar radiation ceases, thereby causing body temperatures (T_b) to drop below the critical levels needed for song production (Sanborn, 1977). ii) Excepting crepuscular species, dawn/dusk chorusing

TABLE 2. Monthly mean ambient temperatures (T_a), temperature gradients during dusk chorus (start to finish), chorus duration's and chorus starts relative to sunset (SS). Data presented as means and standard deviations (in parentheses).

	November 1996	December 1996	January 1997	February 1997	March 1997	April 1997
T. tristigma						
Start T_a (°C)	23.6 (3.0)	24.1 (1.4)	24.2 (1.3)	25.8 (1.1)	24.8 (0.8)	22.8 (1.3)
Finish T_a (°C)	22.5 (2.6)	23.7 (1.2)	23.3 (1.3)	25.0 (1.2)	24.0 (0.8)	22.2 (1.4)
Temperature gradient	1.0 (1.4)	0.4 (0.5)	0.8 (0.6)	0.9 (0.6)	0.8 (0.5)	0.6 (0.6)
Chorus duration (hr)	0.53 (0.17)	0.75 (0.14)	1.79 (0.51)	1.49 (0.57)	0.77 (0.37)	0.44 (0.10)
(Chorus finish - SS) (hr)	0.28 (0.08)	0.30 (0.08)	0.33 (0.05)	0.33 (0.06)	0.36 (0.02)	0.30 (0.06)
n	20	24	24	20	17	16
A. curvicosta						
Start T_a (°C)	23.3 (2.3)	23.7 (1.3)	23.5 (1.2)	25.0 (1.2)	24.5 (0.9)	-
Finish T_a (°C)	23.2 (2.4)	23.5 (1.2)	23.2 (1.2)	24.9 (1.2)	24.4 (0.9)	-
Temperature gradient	0.5 (0.1)	0.2 (0.3)	0.3 (0.5)	(0.2)	(0.1)	-
Chorus duration (hr)	0.20 (0.09)	0.31 (0.08)	0.35 (0.17)	0.24 (0.10)	0.04 (0.02)	-
(Chorus start – SS) (hr)	0.31 (0.05)	0.23 (0.09)	0.21 (0.07)	0.26 (0.10)	0.20 (0.09)	-
n	6	24	24	19	3	-
G. viridis						
Start T_a (°C)	23.2 (2.7)	23.8 (1.3)	23.5 (1.2)	25.1 (1.2)	24.1 (1.3)	22.7 (1.3)
Finish T_a (°C)	22.6 (2.5)	23.6 (1.2)	23.3 (1.2)	24.9 (1.2)	23.7 (1.2)	22.6 (1.3)
Temperature gradient	0.6 (0.7)	0.2 (0.3)	0.2 (0.2)	0.2 (0.3)	0.4 (0.3)	0.2 (0.2)
Chorus duration	0.33 (0.09)	0.39 (0.07)	0.38 (0.09)	0.34 (0.05)	0.30 (0.06)	0.20 (0.05)
(Chorus start – SS) (hr)	0.04 (0.11)	-0.03 (0.11)	0.00 (0.11)	0.01 (0.07)	0.09 (0.04)	0.16 (0.04)
n	21	25	24	20	18	13
C. saundersii						
Start T_a (°C)	22.8 (2.6)	23.7 (1.3)	23.4 (1.2)	24.9 (1.2)	-	-
Finish T_a (°C)	22.3 (2.4)	23.3 (1.3)	23.1 (1.1)	24.8 (1.3)	-	-
Temperature gradient	0.5 (0.8)	0.4 (0.6)	0.3 (0.5)	0.1 (0.2)	-	-
Chorus duration	0.57 (0.14)	0.60 (0.15)	0.70 (0.13)	0.54 ((0.17)	-	-
(Chorus start – SS) (hr)	0.26 (0.06)	0.27 (0.07)	0.26 (0.05)	0.26 (0.08)	-	-
n	20	24	24	16	-	-
G. pluvialis						
Start T_a (°C)	23.1 (2.7)	23.7 (1.3)	23.4 (1.3)	24.8 (1.2)	23.9 (0.8)	22.1 (1.5)
Finish T_a (°C)	22.0 (2.4)	23.1 (1.4)	23.0 (1.2)	24.6 (1.2)	23.5 (0.8)	21.5 (1.5)
Temperature gradient	1.1 (1.7)	0.6 (0.6)	0.4 (0.5)	0.2 (0.5)	0.4 (0.3)	0.7 (0.6)
Chorus duration	1.07 (0.37)	1.00 (0.43)	0.81 (0.24)	0.71 (0.27)	0.81 (0.23)	0.75 (0.29)
(Chorus start – SS) (hr)	0.13 (0.29)	0.24 (0.24)	0.34 (0.16)	0.32 (0.17)	0.37 (0.07)	0.38 (0.08)
n	20	23	23	20	15	16

species produce their main singing periods during the day. iii) During dusk chorusing, cicadas commonly become active, undertaking frequent localised flights to nearby branches or trees. This is especially notable in ♀♀ of *C. saundersii*, corresponding to the period of crepuscular mating activity (Daws et al., 1997). iv) Although overlap of chorusing occurs, species differ in chorus start and finish times. This suggests differing response levels to critical external stimuli (e.g. light intensity) for each species, but these may be modified by differing micro-habitat niches (e.g. dense vs open foliage). v) *C. saundersii* (and apparently other crepuscular species) do not exhibit dawn chorusing. vi) The dusk song of the *T. tristigma* is indistinguishable from the day song, while in *G. viridis* the dusk song is an extended version of the very brief 'whistle' song sporadically emitted during the day. *A. curvicosta* has a continuous coarse dusk song, which is the extended equivalent of the longer phrase emitted as part of the day song. *P. claripennis* produces a

continuous rattling song (which forms a major, but not continuous part of the day song). The dusk choruses of all species are therefore emitted as continuous songs, irrespective of the structure of the day songs. vii) *T. tristigma* systematically changes its late afternoon to dusk calling behaviour through the season, which seems most plausibly related to seasonal temperature patterns. A very general correspondence does exist between the T_a and singing patterns (Fig.8D), as for example, the occurrence of discrete dusk chorusing behaviour during the slightly cooler November and April periods. In contrast, the brief re-occurrence of this behaviour in early February seems to follow a sharp shift to higher T_a. Overall, however, the T_a's occurring during and between the periods of changing behaviour extensively overlap, as reflected in the very similar monthly average T_a's for chorusing (Table 2). Available data are therefore inconclusive as to the role of T_a in explaining the changing behaviour patterns, and imply influence of additional factors.
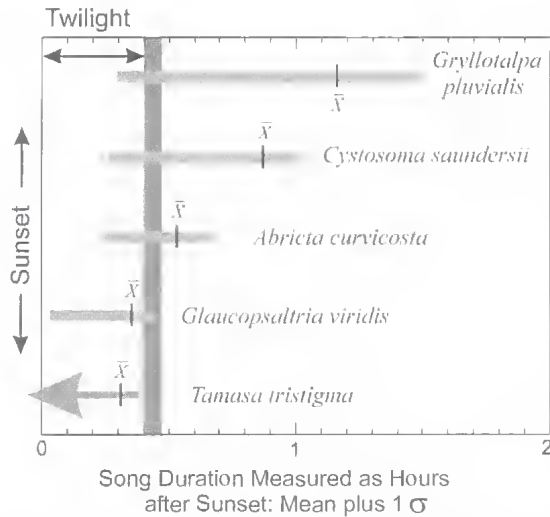
FIG. 9. Summary of dusk chorus duration, relative to sunset, of the five cicada and the mole cricket species. Twilight represents time between the sunset and civil twilight lines, the width of the civil twilight line marking the restricted seasonal variation of twilight through the observation period.

Staicer et al. (1996) listed 12 hypotheses in 3 categories to explain dawn/dusk chorusing in birds: 1) intrinsic to internal state, e.g. hormonal levels; 2) social function; 3) dawn preference resulting from daily timing of environmental selective pressures. Within these categories, the following aspects, in combination, are considered potentially relevant to cicadas:

1) Self-stimulation. Dawn chorusing perhaps represents a 'warming-up' strategy necessary for relatively static species (cf. Josephson & Young, 1979). A possible cue for dawn/dusk song could be the changing xylem-flow pressure within vegetation which stops at dusk and resumes at dawn, presumably responding to transpiration rate (e.g. Dolling, 1991:8). As noted, however, not all cicadas sing at dawn/dusk. 2) Mate attraction, certainly critical for dusk singing crepuscular insects. In other species, however, mating occurs throughout the day, with no observational evidence for unusually high mating activity at dawn/dusk. 3) Mate stimulation. The intensity of dawn/dusk chorusing, plus the optimal acoustic conditions, may facilitate female location of males at a time of lowered predation pressure. 4) Social dynamics. Chorusing may represent an effective mechanism, by signaling, of adjusting spatial distributions between calling males, after

dispersion during the day (e.g. by predation). Doolan & MacNally (1981) have shown that although aggregation is important in C. saundersii for increasing mating success, individuals space themselves at ~1-1.5m apart, with females selecting males only on the basis of their acoustic display. Doolan (1981) further suggests that the spatial distribution results from the interplay between selective pressures to aggregate (ensuring greater numbers of females), and selective pressure to space (enhancing individual success in mating). The short and intense dawn/dusk chorusing provides a mechanism for this to happen and explains the increased, but localised activity of individuals. It also may explain why chorusing is important for relatively localised and also for aggregating species. 5) Lowered predation rates from birds, reptiles, arachnids, and predatory insects. Doolan & MacNally (1981) note the more intense bird predation early in the dusk chorus of C. saundersii. 6) Acoustic transmission enhanced at dawn/dusk, as previously noted. 7) Energy reserves conserved/accumulated during night, stimulating burst of singing at dawn. This does not, however, explain the dusk chorus.

UNIQUENESS OF THE CICADA AND MOLE CRICKET SONGS. As noted, the extensive temporal overlap of songs during the acoustically 'busy' dusk window requires that the songs are species specific. A detailed presentation of the song characteristics is beyond the scope of this paper, but the essential temporal structures of the cicada songs are presented (as oscillograms/ waveform plots) in Young (1972a,b; 1980), Simmons & Young (1978), Young & Josephson (1983) and Ewart (1995). The G. pluvialis call is documented by Otte & Alexander (1983). These data clearly show the distinctive temporal song structures of each species, seen in their pulse and phrase structures, and pulse repetition rates. The differences are also reflected in the dominant frequencies of the songs. For G. viridis, C. saundersii, T. tristigma, A. curvicosta, P. claripennis and G. pluvialis, these frequencies (author data) are, respectively (kHz): 1.8-1.9; 0.8-0.9; 6.1-8.4; 9.5-9.6; 5.9-6.8; and 2.1. Further differences are seen in the detailed structures of the frequency bands, i.e. whether broad or narrow, indicating the 'purity' of the emitted tones. These are represented as bandwidths, based on the sound energy emitted between the lower (25%) and upper (75%) quartiles determined from song spectra. Respective values are: 0.14; 0.28; 1.0; 2.3; 2.1; and 0.27kHz. The G.

viridis song closely approaches a modulated pure tone (see also Young & Josephson, 1983), while the songs of *G. viridis* and *G. pluvialis* exhibit well defined harmonics (to 5f), giving increased transmission flexibility to the songs.

Notwithstanding the extensive synchrony during dusk chorusing between species, the interspecific songs each have their uniquely defined acoustic properties.

ACKNOWLEDGEMENTS

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